

	<i>A. Woodfordi</i> , ♀ adult.	<i>A. flavicollis</i> , ♀ adult.
Back of the neck, back, and scapulars:	Dark chestnut-rufous.	Ashy brown, slightly glossed.
Wing and upper tail-coverts:	Ashy black, fringed with cinnamon-rufous.	Ashy brown.
Whole of the under surface:	Cinnamon-rufous, becoming more cinnamon and less rufous below the breast. Throat and neck flecked with small dark shaft-spots.	Lower part of the cheeks, sides of the throat, and neck cinnamon. Feathers of the chin, front of throat and neck, and chest dull chestnut, shading into dark grey towards the extremities, and somewhat widely and irregularly margined on one or both webs with white. Breast and underparts blackish grey, edged and fringed with whitish or buff on the belly.
Tarsus	3.1.	3.4.
Middle toe	2.7.	2.6.
Claw	2.1.	2.8.

I think anyone taking the trouble to compare the above characters and measurements will have no further doubt that *A. Woodfordi* is a very distinct bird; the proportion of the middle toe and claw to the tarsus shows this at a glance, for in the Solomon-Island bird the tarsus is much the longer, while in *A. flavicollis* it is somewhat shorter.

Oates, in his 'Birds of Burmah,' ii. p. 255, is no doubt somewhat in error in describing the male and female of *A. flavicollis* as similar in plumage, for the female never has the slate-grey upper and underparts so conspicuous in the adult male.

XL.—*A Contribution to the Knowledge of the Dermal Sense-Organs of the Crustacea.* By Dr. OTTO VOM RATH *.

I HAVE been engaged for a long time upon comparative studies on the dermal sense-organs of Arthropods, and have already published accounts of my investigations on Myriapods and

* Translated from the 'Zoologischer Anzeiger,' xiv. Jahrg. no. 365, pp. 195-200, and no. 366, pp. 205-214, June 1891.

Insects*; the following paper is intended to give the most important of the results which I have obtained from the Crustacea. In addition to studying our indigenous freshwater Crustacea† and land Isopods, I availed myself of the opportunity afforded by a sojourn at the Zoological Station at Naples to investigate a large number of marine forms belonging to all the orders and families of which I was able to obtain specimens. My object in so doing was, by comparative studies, both to elucidate the morphology of the several sense-organs, as well as to determine as thoroughly as possible, by means of series of sections, the finer structure of the nerve-end apparatus belonging thereto; for I am of the opinion that an exact knowledge of these relationships is a necessary condition for rational physiological experiments, and that many of the interesting attempts which have been made to determine the function of the sense-organs situated on various parts of the body are not conclusive because sufficient regard has not been paid to other sense-organs of a similar kind.

In the copious literature of the Crustacea we find, as we are all aware, a large number of valuable statements as to individual sense-organs, which, however, in reference to the nerve-end apparatus are not unfrequently contradictory. The reason for these conflicting interpretations may for the most part be found in the fact that very few authors have examined the sense-organs in question by means of sections, and that in examining even the transparent forms confusion may easily take place between the nuclei of the true percipient sense-cells and those of the epidermis-cells. It would be out of place in this short essay to enter into the literature of the subject, yet I would at least recall the important writings of Leydig, Claus, Weismann, Leuckart, La Valette, Hensen, Sars, Hoek, Rougemont, Wrzësniewsky, Gamroth, Haller, Blanc, and Kraepelin. To Leydig the merit is indisputably due of having first described the most important dermal sense-organs in Crustaceans, Myriapods, and Insects.

In the following pages only the most general results of my investigations will be given as briefly as possible: I intend

* O. vom Rath, "Die Sinnesorgane der Antenne und der Unterlippe der Chilognathen," Archiv f. mikr. Anat. 27 Bd. 1886; "Ueber die Hautsinnesorgane der Insecten," Zeitschr. f. wiss. Zoologie. 46 Bd. 3 Heft, 1888.

† Among the higher Crustacea I have paid special attention to *Astacus fluviatilis*, and have examined the whole of its dermal sense-organs; as the hardness of the chitin presents great difficulties to the scalpel, I employed for the purposes of dissection as far as possible specimens which had just moulted and were still fairly soft.

shortly to publish a more detailed account, accompanied by figures.

Owing to the usually extremely hard chitinous body-covering of the Crustacea, a sensory perception, with the exception of sight, can only be conveyed by means of structures composed of hairs. In many cases such sensory hairs are externally in no way distinguishable from ordinary hairs and are characterized as sense-organs only by the sense-cells lying beneath their base; in many instances, however, they have peculiar shapes, and have been described as feathered setæ*, half-feathered setæ, cones, knobs, clubs, plugs, threads, styles, cylinders, tubes ("Fiederborsten, Halbfiederborsten, Kegel, Kolben, Keulen, Zapfen, Fälen, Griffel, Cylinder, Schläuche"), &c. Yet, however different and varied the form of the sensory hairs of the Crustacea, they are nevertheless connected together by a continuous series of transitions. The first antennæ of the Copepods are of especial interest, since we often find upon them placed close together the greatest variety of sensory hairs with the various intermediate forms.

At the spot where any kind of capillary structure, it matters not whether a sensory or an ordinary hair, projects from the cuticle, the latter is pierced by a more or less fine pore-canal. The mode of attachment of the hair is of the greatest functional importance; in the majority of cases the capillary structures rest upon a more or less arched, cupola-shaped, chitinous membrane, which rises from the margin of the pore-canal; this membrane is sometimes soft and thin, so that it gives great mobility to the hair, as is above all characteristic of the auditory hairs. The shaft of the hair is generally in two parts, and consists of a stouter chitinized proximal and a paler thin-walled distal portion, the two being distinctly separated from one another by a slight constriction.

I. ON THE OCCURRENCE OF DERMAL SENSE ORGANS ON THE BODIES OF CRUSTACEA.

In the whole of the Crustacea belonging to the different classes, orders, and families I have discovered sensory hairs on almost all parts of the body. Both the first as well as the

* Feathered setæ are, as is well known, widely distributed among the Crustacea and also occur in the aquatic Dipterous larvæ; I would, however, incidentally remark that feathered setæ are also found in genuine land-animals, *e. g.* on the anterior portion (so-called tongue) of the hypopharynx of *Scutigera*, on the palp-shaped appendages of the maxillæ of *Lithobius*, and on the pedipalpi of male spiders.

second pair of antennæ and their squamæ, the whole of the mouth-parts, and all the pairs of limbs are the bearers of numerous sensory hairs; in a similar way I always found sensory hairs at the end of the tail, on the margin of the last abdominal segment; in rarer instances free sensory hairs are also found on the segments, *e. g.* in *Branchipus*. The sensory hairs of the mouth-parts and legs have hardly been noticed at all by authors, and I know of no precise statements in literature with reference either to their arrangement and shape or to the finer histological structure of the nerve-end apparatus; the sensory hairs of the antennæ, on the other hand, have been described by a number of writers.

Before passing on to speak of the various sensory hairs, I would remind the reader that the whole of the jointed appendages of the Crustacea, with the exception of the first antennæ, are reducible to the typical biramose limb, and in the following pages I shall employ the convenient expressions—protopodite (shaft), exopodite (outer branch), and endopodite (inner branch).

a. Sense-Organs of the Antennæ.

The antennule, or first antenna, is the bearer of the most important sensory hairs, since upon it are found both the so-called olfactory tubes ("Riechschläuche") and also, at least in the Decapods, the auditory organs; besides these we find on the most widely different regions of this first antenna sensory hairs of various shapes, which are regarded as tactile organs. Tactile hairs, which run to a sharp point and are not feathered, are found distributed with a certain amount of regularity in the immediate neighbourhood of the olfactory tubes, and act to a certain extent as protecting setæ. The number and arrangement, as well as the outward form and size, of the olfactory tubes are extremely varied and characteristic in the orders and families, and to a large extent even in the different species. In certain cases a number of them are found on the terminal joint only of the first antenna, *e. g.* in *Idothea*; frequently they are collected in bundles on several joints, *e. g.* in *Astacus*; but it is not unusual to find a single structure of the kind only on several joints, *e. g.* in *Caprella*.

It is worthy of note that in the male sex the size and number of these organs is much more considerable than in the female, and it was shown by Weismann* for *Leptodora* and

* Weismann, "Ueber Bau- und Lebenserscheinungen von *Leptodora hyalina*," Zeitschr. für wiss. Zool. 24 Bd., 1874.

by Claus * for *Nebalia* and *Phronima* that it is not until the animal arrives at sexual maturity that they attain their full number. In a similar way it has long been known that in blind Crustacea the number and size of the olfactory tubes is more considerable than in their allies with full visual power, e. g. in *Asellus cavaticus* and *Gammarus pulex*. The mode of attachment of the olfactory tubes to the cuticle is of such a kind as to exclude any great degree of mobility for the hair, and we can therefore hardly suppose them to be auditory organs. Whether the usually bluntly rounded distal end of the structures we are discussing is closed by a delicate membrane, as Claus insists, or is open, as stated by Leydig, is difficult to determine. The hair appeared to me to be closed in many cases and open in others; moreover, these extremely delicate structures are often damaged at the tip. I would on no account advise treating these organs with liquor potassæ, since I have often convinced myself, in the case of Myriapods, Insects, and Crustacea, that after boiling unmistakably closed olfactory cones or tubes in a weak solution of potash a distinct opening became visible, since the delicate closing membrane had simply disappeared. I have, however, been able to determine by a series of experiments that in Crustacea the closing membranes of the olfactory tubes are so thin as to present no obstacle to delicate sensation, while fluids are able to penetrate them very easily, and to come into direct contact with the nerve-end apparatus. Into a saturated aqueous solution of *bleu de Lyon*, or methylene blue, I put a large number of small living Crustacea, e. g. *Asellus*, *Gammarus*, and different species of Cladocera, and then fished out specimens at different intervals, some after one hour, others later. A stay of three to four days in these dyes does not injure an *Asellus* in the least; on the contrary, on being washed in fresh water and examined under the microscope these Isopods appear perfectly lively. In the animals upon which I experimented the tips of the olfactory tubes had invariably become coloured first; the dye then gradually spread as far as the base of the hair, and after a longer period had elapsed the nerve-end apparatus was also found to have become stained. I made a similar experiment upon larger Crustacea, such as *Astacus*, by cutting off from the living animal the first antenna at its base and laying it in the solution. Staining at once began to take place at the tips of the olfactory tubes, and then penetrated slowly downwards. As a matter of course,

* Claus, "Ueber den Organismus der Nebaliiden und die systematische Stellung der Leptostraca," *Arbeiten aus d. Zoolog. Institut der Univ. Wien*, 1889; "Der Organismus der Phronimiden," *ibid.* 1879.

before commencing my experiments I was careful to ascertain that all the olfactory tubes were intact.

With the auditory organ situated in the basal joint of the first antennæ of the Decapods I shall deal very shortly, and refer the reader to Hensen's* detailed description. This author distinguishes otolith-hairs, free hairs in the auditory sac, and free hairs situated upon the surface of the antennæ. Characteristic for all auditory hairs is their mode of attachment, in that the shaft, which is always feathered, stands upon an extremely delicate cupola- or dome-shaped membrane, in consequence of which the hair is able to swing to and fro with the greatest ease, and can be set in motion by waves of sound. According to Hensen, "the auditory hairs stand upon a pore-canal, the walls of which develop on one side a larger or smaller thickening, the tooth. All hairs exhibit at one portion of their proximal end a peculiar process, the ligula, to which the nerve is attached." Contrary to Hensen, in examining my extensive material I not unfrequently met with feathered hairs, occupying an intermediate position between typical, freely mobile, auditory hairs, and feathered, stiff, unmistakably tactile hairs, resting upon a strongly chitinized cupola-shaped membrane, so that it was a moot point whether such transitional forms were to be regarded as auditory or tactile hairs.

Among tactile hairs, always ending in a sharp point, there are found upon the first antennæ unfeathered, half-feathered, completely feathered, and toothed sensory hairs.

In the first antenna of *Nebalia* there spring from a four-jointed shaft two branches, of which the one is flagelliform and bears the typical olfactory tubes, while the other is expanded into a squamiform plate, the margin of which is beset with a large number of long, fine, sharply pointed sensory hairs, which are not plumose, but rather finely denticulate.

Incidentally I would just allude to the fact that upon the antennæ of certain Amphipods peculiar hairs have been found, the so-called "*calceoli*." These shoe-like appendages, the physiological importance of which is still obscure, are by no means confined, as was formerly supposed, to the flagellum of the lower antennæ of the male, but occur, as has been shown by later investigations, in some forms in the female sex also, and, moreover, on both pairs of antennæ.

The sensory hairs of the *second antenna* are of far less

* Hensen, "Studien über das Gehörorgan der Decapoden." Zeitschr. für wiss. Zool. 13 Bd., 1863.

importance than those of the first *. Typical olfactory tubes have been discovered upon the second antennæ, which are also designated tactile antennæ, only in *Nebalia* and *Diastylis*, through the researches of Claus.

Tactile hairs, however, occur in abundance upon the second antennæ, and may exhibit great differences in number, size, and shape, while here and there they constitute forms which are transitional to the olfactory tubes. To this category also belong the cylinders or clubs of the lower antennæ of *Gammarus puteanus* (Leydig). Whether the plugs which are found at the tip of the large (second) antennæ of the woodlice have the value of a more highly differentiated sense-organ, or whether they likewise are tactile in function, has not been decided. It is also not unusual to find upon the second antennæ feathered hairs which are easily movable and stand freely upon the surface, and which, judging by the analogy of their general appearance, might be regarded as auditory. To the sensory hairs of the second antennæ likewise belong the feathered hairs standing on the edges of the squamæ in the higher Malacostraca; I determined the presence of the group of sense-cells belonging to each of these hairs in the case of *Mysis*, *Siriella*, *Squilla*, *Palaemon*, and *Astacus*.

b. Sense-Organs of the Mouth-parts.

As I have found in Myriapods and Insects sense-organs in the buccal cavity and upon the mouth-parts which, according to their position and form, were best interpreted as organs of taste, it was a natural idea to search for such sense-organs in the Crustacea also in the region of the mouth-parts. I was able to determine that in all the species I examined, belonging to the most widely different orders and families, the mouth-parts always bear a large number of sensory hairs of various shapes, generally feathered and pointed at the tip, which I would regard as tactile bristles; I was never able to find hairs, however, which could be compared with the olfactory tubes of the antennæ, or which, in consequence of their general appearance, could be interpreted as gustatory or olfactory organs. In the cases where the mandible carries a palp this organ exhibits at the tip a large sensory field beset with many hairs, *e. g.* in *Astacus*; in both pairs of maxillæ of all Crustacea sensory hairs are closely packed on the exo- and endopodites as well as on the lobes. In the case of *Astacus* I further

* I may remind the reader that the second antennæ may be atrophied into a stump, *e. g.* in *Thronina*.

found that, in a similar way, the first three thoracic appendages also, which are termed maxillipedes or accessory maxillæ, are richly provided with sensory hairs on the exopodites, endopodites, and lobes (first maxillipede). Owing to the agreement shown by these discoveries I considered it *à priori* probable that all the pairs of appendages belonging to thorax and abdomen would have their sensory hairs.

c. *Sense-organs of the Thoracic and Abdominal Appendages (Pleopoda).*

The presence of sensory hairs upon the whole of the extremities I determined successively in the Phyllopoda (*Branchipus* and *Apus*), Cladocera (*Daphnia*, *Sida*, *Moina*), Copepoda (*Diaptomus*, *Cyclops*, *Calanus*), Amphipoda (*Phronima*, *Hyperia*), Isopoda (*Anilocra*, *Cymothoa*, *Idothea*), Schizopoda (*Siriella*, *Mysis*), and Decapoda (*Astacus* and *Palaemon*). In the case of biramose appendages, sense-organs are found upon the exopodite as well as the endopodite. In the Cirripedia (e. g. *Lepas*) I found that the whole of the hairs upon the cirriform limbs were sensory. In the Arthrostraca and Thoracostraca the abdomen consists, as we know, of seven segments, of which the first six usually bear pairs of limbs (pleopoda), while the telson, or seventh segment, is always apodous. Even the telson is provided with sensory hairs. I cannot here enter upon a closer description of the sensory hairs of the several appendages in the different families and species. The auditory organs situated in the endopodite of the last pair of pleopoda, the so-called tail, of the Schizopods *Siriella* and *Mysis* are provided with otolithic hairs, possessing the characteristic peculiarities described above in the case of the auditory hairs of the first antennæ. In the Schizopods we also find free auditory hairs upon the surface of the tail.

d. *Free Sense-organs upon the Segments.*

Under this head I merely make passing allusion to the fact that in a few rare cases free sensory hairs have also been described as existing upon the somites, and have been held to be tactile in function. Weismann found feathered tactile setæ standing in pairs upon the dorsal surface of the fourth abdominal segment of *Leptodora*, and Claus alludes to similar free tactile bristles upon the somites of *Branchipus*.

II. HISTOLOGICAL STRUCTURE OF THE NERVE-END APPARATUS OF THE SENSORY HAIRS OF CRUSTACEA.

The histology of the nerve-end apparatus of the various sensory hairs, whether olfactory tubes or tactile hairs (smooth, half-feathered, completely feathered, or toothed), is essentially the same, and corresponds most minutely with what I have previously described for Myriapods and Insects. My interpretation of the finer structure of the nerve-end apparatus of the sensory hairs of Arthropods differs somewhat from the statements of other authors.

In the Crustacea, beneath the base of each capilliform structure serving a sensory function, there lies a group of cells which is connected with a nerve; these cells are termed a ganglion by authors; but since they are manifestly the percipient epithelial cells, I prefer to term them sense-cells, without, however, intending thereby to insist on a strict physiological distinction between ganglion- and sense-cells. In very rare cases only, *e. g.* in the whole of the sensory hairs of the cirriform feet of *Lepas*, I found beneath the hair only a single bipolar sense-cell, of relatively large size and elongate in form, with a roundish nucleus which considerably exceeded the nuclei of the cells of the hypodermis in size. According to the usually accepted view, the nerve which is connected with the ganglion-cells is supposed to traverse the entire length of the ganglion and then enter the sensory hair. I have been able in a very large number of cases, *e. g.* in the olfactory tubes of *Astacus**, to convince myself with absolute certainty of the fact that the nerve in no way passes through the group of sense-cells, so that the sense-cells are attached to the nerve-fibrils much as the grapes in a bunch; on the contrary, the nerve splits up beneath the group of sense-cells and gives off a fibril to each cell. In the anterior or distal region of the group of sense-cells I then distinctly saw the way in which the protoplasmic prolongations of the various cells unite into a finely streaked bundle, the *terminal cord*, which actually enters the hair, while its fibrillate nature can often be distinctly recognized right to the tip of that structure. Strictly speaking therefore the sensory hair does not contain a true nerve, but rather the united prolongations of sensitive epithelial cells; it follows therefore that we can scarcely speak of a true axis-cylinder or axis-fibre. The

* An olfactory tube of *Astacus*, with the nerve-end apparatus belonging thereto, has already been described and figured by me in my previous publication (Archiv f. mikr. Anat. 27 Bd., 1886).

lumen of the sensory hair, however, is by no means exclusively occupied by the terminal cord; I observed in many cases, and with especial distinctness in the olfactory tubes, that the hypodermis-cells send distinct processes into the hair; the cells which do this are those which form the matrix of the hair. The number of sense-cells belonging to each sensory hair varies very much: in the case of the Decapods I was always able to count a large number of them, but in the Phyllopods and Cladocera only a few. The groups of sense-cells are sometimes rounder, sometimes more elongate or linear in shape. The nuclei of these cells are usually round and possess a corresponding network of chromatin-fibres; they are readily distinguishable from the more elongate and always darker-coloured nuclei of the hypodermis. It is only shortly after ecdysis (as is seen especially clearly in *Astacus*) that the difference in external appearance between the nuclei of the hypodermis-cells and those of the sense-cells is small. The group of sense-cells often lies a very long way from the hypodermis and the sensory hair, and the terminal cord is then of considerable length*, as, for instance, in the first antennæ of the Caridinæ and Brachyura. Each group of sense-cells is surrounded by a sheath, which consists of flat cells with flattened nuclei, and appears as a continuous prolongation of the neurilemma of the nerves. It can usually be distinctly seen that this sheath also surrounds the terminal cord. I believe that the cells of the sheath do not essentially differ from those of the hypodermis. When the groups of sense-cells are collected in greater numbers near one another, and lie at some little distance from the sensory hairs, we always detect between the terminal cords elongate dark-coloured nuclei, which belong to elongated hypodermis-cells. From these cells it is not always easy to distinguish those of the above-mentioned sheath of the terminal cord. If the sensory hairs, as is often the case, are united into a bundle, or stand close together in larger numbers upon a common sensory field, the groups of sensory cells belonging to the separate hairs may be compressed into a compact mass. Even then, however, the separate elongated groups or bands of sense-cells can be distinguished with tolerable clearness within the apparently single ganglion, and we observe between them the flat nuclei belonging to their sheaths of connective tissue. The terminal cords, too, are approximated to one another, and between them lie flat nuclei, which belong partly to the

* In the Insects the group of sense-cells is usually found in the neighbourhood of the hair, and is even frequently situated within the hypodermis.

connective-tissue sheaths of the terminal cords, and partly to the intermediate hypodermis-cells, but in no case justify the assumption of the existence of a second anterior ganglion. I would remind the reader that I have already proved, in connexion with the Myriapods and Insects, that in all cases in which authors, *e. g.* Szazepin, have described two ganglia lying one behind the other, *e. g.* in the antennæ of the Chilognatha and the Wasp, in reality only a single group of sense-cells exists. In a similar way I convinced myself in the case of the Crustacea that in those instances in which it was stated by authors that the nerve-end apparatus consisted of two ganglia lying one behind the other (first antenna of the Daphnids and Phyllopods according to Leydig, first antenna of *Leptodora* according to Weismann), or that one ganglion was divided into two parts connected by nervous matter (large or second antenna of the Woodlice according to Leydig*), in reality only one ganglion, that is a single group of sense-cells, is to be found; and that hypodermis-cells have been mistaken for a second distal ganglion. Moreover we may get the false appearance of two groups of sense-cells lying one behind the other, owing to the fact that tactile hairs also are usually found in the immediate neighbourhood of the olfactory tubes, and that, even in sections, the group of sense-cells belonging to the former are always closer to the hypodermis than those of the latter. We find the most interesting structural conditions of the nerve-end apparatus among the Entomostraca. I have already remarked that the whole of the sensory hairs of the cirriform feet of *Lepas* show only a single large sense-cell beneath their base, while hitherto in all other cases I have always found a group of sense-cells beneath the sensory hair†.

* Leydig, "Ueber Amphipoden und Isopoden," Zeitschr. f. wiss. Zool. 30 Bd. Suppl., 1878; "*Artemia salina* und *Branchipus stagnalis*," *ibid.* 3 Bd., 1851; "Naturgeschichte der Daphniden," 1860; "Geruchs- und Gehörorgane der Krebse und Insecten," Archiv f. Anat. u. Phys. 1855; "Die Hautsinnesorgane der Arthropoden," Zool. Anz. 9 Jhg., nos. 222 and 223, 1886.

† Among Insects the instances in which only a single sense-cell belongs to a hair are also by far the most unusual, and, in addition to the cases described and figured by me, occur chiefly in the sense-organs of the halteres of Diptera, as has recently been shown by Weinland. In his paper on the balancers (halteres) of Diptera (Zeitschr. f. wiss. Zool. 51 Bd., i. Heft) Weinland, among other things, describes the histology of the sense-organs belonging to the halteres, and states that, in connexion with each of these different sense-organs, a bipolar ganglion-cell is always found. Weinland further says:—"That several ganglion-cells send out from among them only a single nerve-ending, as has been stated by vom Rath to be the more usual occurrence in Insects, is at any rate not the case in the nerve-end apparatus of the halteres; Künckel's view is in this

As regards the sense-organs of the Phyllopods, e. g. *Branchipus*, the views of authors are divided. According to Leydig (*loc. cit.*) and Spangenberg*, two ganglion-cells, lying one behind the other, belong to each sensory hair; Claus† was able to distinguish only one ganglion-cell; in connexion with the sensory hairs of *Branchipus* I always counted from three to four cells, and from four to five beneath those of *Apus*. With the sensory hairs of both these Phyllopods I shall subsequently deal at greater length. Among the Cladocera the number of sense-cells belonging to each sensory hair is also tolerably small.

As regards the histological structure of the nerve-end apparatus of the auditory organs, this in no way differs from the description which I have given above. I am unable to confirm the statements of authors (e. g. Hensen, *loc. cit.*), who ascribe only a single ganglion-cell to each auditory hair; on the contrary, I always found beneath the base of each auditory hair of *Astacus*, *Siriella*, and *Mysis* a distinct group of sense-cells, with terminal cords reaching to the tip of the hair.

I would here just mention in passing that behind the groups of sense-cells in the Crustacea I have never found those peculiar large cells of glandular appearance, such as I have described as *companion cells* ("Begleitzellen") in the case of the sense-organs of Myriapods and many Insects; nevertheless in the neighbourhood of the Crustacean dermal sense-organs there occur, with a certain degree of regularity, on both pairs of antennae, as well as on the whole of the limbs, irregular groups of typical gland-cells, which are particularly noticeable in the Amphipoda and Isopoda.

instance perfectly accurate." The latter remark is liable to be misunderstood. I therefore lay stress upon the fact that Künckel is certainly in error in holding that in Insects invariably only a single ganglion-cell belongs to all sensory hairs. There are isolated cases, it is true, in which only a single sense-cell is found in connexion with each sensory hair, and I may refer the reader to my statements (Zeitschr. f. wiss. Zool. 46 Bd. 3, pp. 416-419) and figures (figs. 3b, 10, 16, 32). At that time I had not included the sense-organs of the halteres within the scope of my investigations; since then I have convinced myself by means of series of sections that it is actually true that only a single large bipolar ganglion-cell belongs to each sense-organ.

* Spangenberg, "Zur Kenntnis von *Branchipus stagnalis*," Zeitschr. f. wiss. Zool. 25 Bd. Suppl., 1875.

† Claus, "Untersuchungen über die Organisation und Entwicklung von *Branchipus* und *Artemia*," Arbeiten aus d. Zool. Institute d. Univ. Wien, 1885.

III. THE PHYSIOLOGICAL IMPORT OF THE DERMAL SENSE-ORGANS.

In discussing the physiological function of the dermal sense-organs of Crustacea we must as far as possible guard against anthropolomorphic conceptions. It is advisable to define the sensations by means of their physical or chemical causes. The perception of an image originating in the eye we term sight, the perception of the waves of sound, hearing, while the perception of the different kinds of resistance to pressure and many other mechanical influences we call touch. In the case of aquatic Crustacea it appears to be a matter of choice whether we speak of the perception of chemical substances dissolved in the water as smell or taste. Crustacea possess no sense-organs within the buccal cavity which, by virtue of their position, we could explain as organs of taste, and those sense-organs situated outside the buccal cavity (upon the antennæ) which are adapted to the perception of chemical substances dissolved in water may serve equally well for the detection and taste of food-matter as for the perception of any other stimulus depending upon chemical influence. I therefore see no reason, in the case of Crustacea which live in water, for drawing a distinction between taste and smell. We should exercise the greater caution in wishing to recognize in Crustacea the same sensations which are experienced by human beings, since the structure of the sense-organs is fundamentally different in the two cases, while even the biological purposes which the sense-organs serve can only coincide to a limited degree. It is very possible that the Crustacea possess senses entirely unknown to us, as, for instance, a sensation which is affected by the amount of oxygen in the water*. It is perfectly certain that the degree of acuteness as well as the extent of the sensations, that is the limits within which perceptions are possible for the various senses, vary extraordinarily in different animals. The eye of a bird of prey and the olfactory organ of a dog far surpass in acuteness of perception the respective sense-organs in the human being. It is well known that many Insects perceive rays of light and waves of sound which have no effect upon our own sense-organs.

We will now discuss the question as to how far we may draw conclusions from the morphological structure of the sense-organs as to the physiological functions of the senses.

* The Crustacea possess sense-organs the function of which is veiled in obscurity, *e. g.* the frontal organ of the Entomostraca.

The nerve-end apparatus is so similar in structure in the different sense-organs that, as it seems to me, it cannot be made use of for this purpose; we have therefore to consider in the first place the form and mode of attachment of the hairs, as well as their number and position. Those capilli-form structures which do not terminate in a sharp point, and which at their distal, usually paler, and thin-walled end, as is shown by the experiments detailed above, permit the entrance of chemical substances dissolved in water, will at once, with some degree of probability, be explained as olfactory or gustatory organs. Those plumose hairs which rest upon an unusually delicate domed membrane, and which are therefore very easily set swinging, are regarded as auditory organs. Those sensory hairs which in all probability serve neither the olfactory nor auditory function are designated tactile setæ. In drawing these distinctions it is by no means maintained that the functions specified are so sharply delimited from one another, and that possibly the same hair may not serve in several of the above-mentioned capacities at once. Let us now enquire how the various organs are distributed upon the body.

The olfactory organs (olfactory tubes) are situated exclusively upon the first antennæ in all the Crustacea which we have examined, with the exception of *Nebalia* and *Diastylis*, in which they occur upon the second antennæ also. In my opinion these organs probably serve in the first place to scent out food and the opposite sex; in the case of the aquatic forms they would have the general function of testing the chemical conditions of the water. In exclusively terrestrial Crustacea, *e. g.* the Woodlice, they would in all probability enable the animal to find out the constitution of the atmosphere, and in this sense might be designated olfactory organs. In discussing the olfactory tubes we must also allude to the fact that they are more powerfully developed in the blind Crustacea than in their nearest allies possessing eyes; and the interesting circumstance that these organs are usually more numerous and larger in the sexually mature male than in the female is also worthy of notice. The theory has often been advanced by authors that the females at the period of maturity of the ova emit a glandular secretion, which is detected by the male by means of his olfactory organs. In the case of the freshwater Copepods, Vosseler* states it as a fact that "the females are discovered and fertilized by the males at night, and even by day, the male must possess other

* Julius Vosseler, 'Die freilebenden Copepoden Württembergs,' Dissertation. Stuttgart, 1886.

means of assistance in addition to his feebly developed eyes, to enable him to distinguish the sexes in pools where the water is often quite turbid." An auditory function on the part of the organs of scent or smell is negatived by the circumstance that, on the one hand, auditory organs could hardly be of special use to the Crustacea in the search for food and in scenting out the other sex, and, on the other, that the mode of attachment of these capilliform structures is of such a kind that they could not well be set swinging and perceive sound-waves.

Into a discussion of the question of the power of hearing in the Crustacea I will not enter here. As regards the higher forms, the Decapods and Schizopods, we have the minute investigations and careful experiments of Hensen (*loc. cit.*), which prove that these higher Malacostraca at any rate possess a very fine sense of hearing. Moreover, it has recently been rendered very probable by the interesting experiments of Delage* that the auditory organs of the Decapods and Schizopods at the same time serve yet another function, in providing for the orientation of the position of the body and the regulation of the equilibrium. Whether and to what extent the Arthrostraca and Entomostraca are able to hear, that is to perceive waves of sound, is, according to our present knowledge of the subject, still very uncertain.

All the sensory hairs which we are not inclined to regard as olfactory or auditory are termed simply tactile organs. To this category belong certain sensory hairs of the first antennæ, and most of those upon the second antenna and its squame; in addition to these all the sensory hairs of the mouth-parts, legs, and caudal appendages, and, finally, all the free sensory setæ upon the somites. Just as the form and arrangement of these sensory hairs, which we call tactile organs, present the greatest variety in the different families and species, while not unfrequently several tactile hairs completely different in shape are found close together upon a certain part of the body in the same animal, so must we make a distinction between the functions of these capilliform structures, and, in addition to coarser and finer tactile sensations, assume the existence of a large number of the most widely different gradations, which our perceptions are certainly unable to appreciate.

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* Delage, "Sur une fonction nouvelle des otocystes comme organes d'orientation locomotrice," *Archives d. zool. expérim.* 1887 (2) t. v. p. 1.